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The geographic distribution of Costa Rican velvet worms (Onychophora: Peripatidae)

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Abstract: Velvet worms, "peripatus" or onychophorans, are "living fossils" that were geographically widespread in Cambrian seas but now occur exclusively on terrestrial habitats. The only extant species studied in some detail are those from Costa Rica, but their real geographic distribution was in urgent need of revision. To solve this problem we visited the localities mentioned in all the original taxonomic descriptions and redescriptions. These visits covered a 25 year period (1988-2014) and included interviews with local residents. We also examined all Costa Rican collections, and checked the information in old maps and books. Here we critically review geographic data, correct errors, assign neotype localities, report on the survival of populations after heavy volcanic eruptions or urbanization, and present the correct geographical distribution for the seven currently described Costa Rican species. Rev. Biol. Trop. 64 (4): 1401-1414. Epub 2016 December 01.

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Velvet worms, also known as "peripatus", or onychophorans, are "living fossils" that have been documented as fossils since their Cambrian origin in China and Canada (Monge-Nájera & Hou, 1999). The phylum Onychophora unites the primitive features of "worms," such as Nematoda and Nematomorpha, with those of the arthropods (Grimaldi & Engel, 2005). Modern velvet worms are classified in two families, Peripatidae and Peripatopsidae. The early diversification of these groups pre-dates the break-up of Pangaea, maintaining regionalization even in landmasses that have remained contiguous throughout the history of the Onychophora (Murienne, Daniels, Buckley, Mayer, & Giribet, 2014).

Their extraordinary biology includes the only true placenta known from an invertebrate, and the production of a hunting adhesive net that is self-assembled in a fraction of a second (Bouvier, 1905; Morera-Brenes & Monge-Nájera, 2010; Concha, Mellado, Morera-Brenes, Costa, Mahadevan, & Monge-Nájera, 2015). Despite their extraordinary biology and their uncertain location in the phylogeny of life (e.g. Podsiadlowski, Braband, & Mayer, 2008; Rota-Stabelli et al., 2010) little is known about them, probably because they have low population densities, with the exception of some areas in New Zealand. In the rainforests of tropical and temperate zones, they live under rotten trees, stones, moss, leaf litter, rotting wood, crevices in the soil and ant and termite tunnels (Grimaldi & Engel, 2005). Their rarity is the main cause most biologists never see them alive. For most of the approximately 200

known species, there is no information whatsoever about their ecology, physiology, behavior, embryology or other aspects.

Research work has focused mainly on species that inhabit the small Central American country of Costa Rica (Morera-Brenes, 2012). Nevertheless, the knowledge of Costa Rican species is preliminary, fragmentary and troubled by outdated taxonomy and serious doubts about the true geographic distribution of each species. The first described onychophorans from Costa Rica were collected in the Nineteenth Century around San José, capital of the country, by the Alsacian naturalist Paul Biolley. At that time, "around San José" could be just a few blocks away from the current center of the city (Hilje, 2013, p. 477). The currently known species are *Epiperipatus isthmicola* (Bouvier 1902a); *Epiperipatus biolleyi* (Bouvier 1902b); *Peripatus ruber* Fuhrmann (1913); *Macroperipatus valerioi* Morera-Brenes & León (1986); *Epiperipatus hilkae* Morera-Brenes & Monge-Nájera (1990); *Peripatus solorzanoi* Morera-Brenes & Monge-Nájera (2010) and *Principapillatus hitoyensis* Oliveira, et al. (2012a). Recent work (Oliveira, Read, & Mayer, 2012b) concluded that the real geographic distribution of Costa Rican species needed urgent revision. In this article we provide that revision and correct several taxonomic and biogeographic errors that were undetected in the scientific literature for more than a century.

MATERIALS AND METHODS

To review the collecting localities of all described Costa Rican velvet worms we visited in eight field trips (September 1988, July 1991, September 1996, October 2004, June 2009, November 2010, October 2012, November 2014) the areas mentioned in the original taxonomic descriptions as well as in redescriptions. These visits cover a 25 year period (1988-2014).

Following the standard procedure for onychophorans (e.g. Bouvier, 1905), in every reported locality (San José province: cantón of San José, cantón of Moravia, cantón of Vázquez de Coronado, cantón of Goicoechea; Puntarenas province: cantón of Parrita; Guanacaste province: cantón of Nicoya; Limón Province: cantón of Siquirres, cantón of Limón), we searched manually under stones, inside and under fallen trees, partially decomposed trunks, as well as under moss covering the ground and trees. Every visit day, at least two of us searched for half a day or more, and as a result collected a little less than 200 specimens in total.

In every locality we also asked verbally to the local residents about their knowledge, including name, folkloric beliefs and any other information that they might have. Additionally, we examined all specimens in all Costa Rican collections: INBio (Instituto Nacional de Biodiversidad), UNA (Universidad Nacional; both in Heredia Province) and UCR (Universidad de Costa Rica; San José Province). We checked the information in old maps and books in the libraries of UNA and UCR, as well as online information through Google.com, and consulted an expert in the history of Costa Rican science (Jaime García, UCR), a professional field collector (Francisco Morales, INBio) and a field zoologist who knows both the animals and the historic locations (Bernal Rodríguez, UCR).

RESULTS

The following revision of all onychophorans described from Costa Rica (Fig. 1) is organized chronologically and includes synonyms, type information, language of original description, and English translation of the most important characteristics (until now, research has been hindered by the use of several languages in the older literature about this group). We have summarized our revision of all Costa Rican species in Fig. 2 and Fig. 4. Both support our statement that Bouvier's (1902a, 1902b) original descriptions differ from his later work (Bouvier, 1907a):

Fig. 1. Graphic catalogue of all described species of Costa Rican Onychophora. **A.** *P. solorzanoi*, photograph by Alejandro Solórzano; **B.** *E. isthmicola*, by Adrián Cabrera, **C.** *P. ruber*, by Bernal Morera-Brenes, **D.** *E. hilkae,* by Hilke Ruhberg; **E.** *P. hitoyensis,* by Georg Mayer, **F.** *E.biolleyi*, by Bernal Morera-Brenes**;** and **G.** *M.* cf. *valerioi*, by José Barquero-González.

Epiperipatus isthmicola (Bouvier, 1902)

Synonyms: *Peripatus nicaraguensis* var. *isthmicola*, by original designation (Bouvier, 1902a: 240); *Peripatus* (*Epiperipatus*) *isthmicola* (Clark, 1913: 18); *Epiperipatus isthmicola* (Stewart B, P., 1900: 345).

Holotype: The holotype was not clearly designated in the original description (see Remarks).

Described type locality: COSTA RICA, "near [the city of] San José, around 1 100 m above sea level". July 1900, P. Biolley col. (Bouvier 1902a).

Neotype locality: COSTA RICA, San José Province, cantón of San José, distrito Hospital, Barrio Cristo Rey, formerly Premontane Moist Forest in Holdridge's (1978) system, 9° 55' 29.90"N - 84° 5'5.03" W, 1 143 m.a.s.l., 27 May 2012, col. A.A. Cabrera Alvarado.

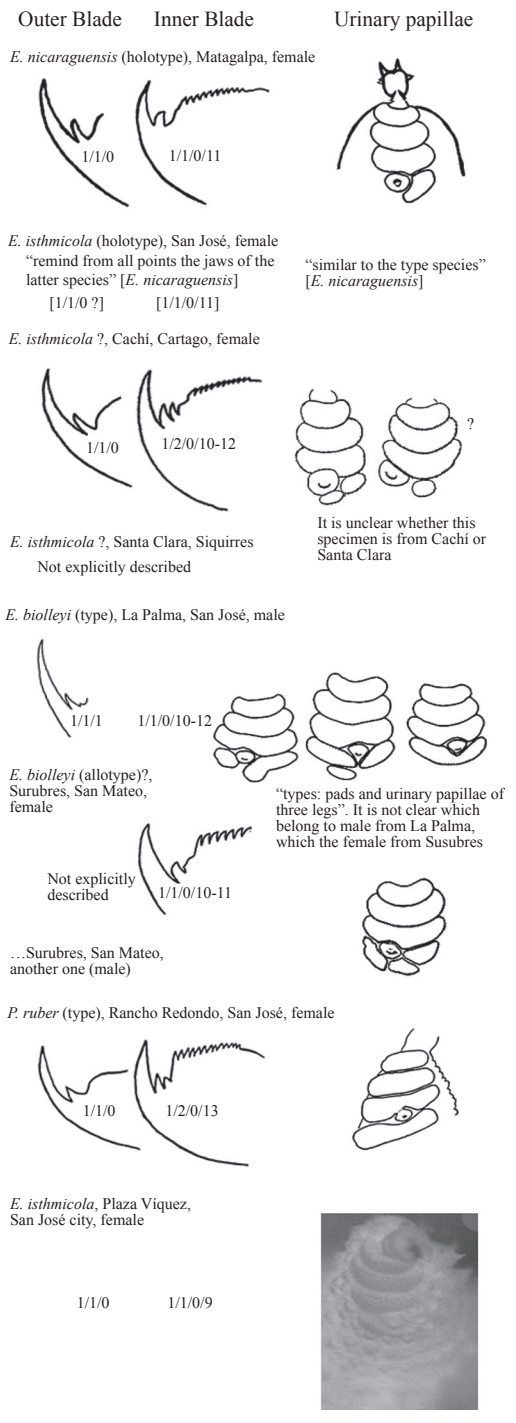

Fig. 2. Comparison between outer, inner blade and urinary papillae of the seven currently described Costa Rican Onychophoran species.

Language of species description: French.

Relevant taxonomic characteristics in the holotype description: "female color blackberry [original French: *mûre*] [decolored in alcohol], of a smaller size, it comes from Costa Rica, where it was captured some two years ago. The dorsal flank of this specimen has a perfectly uniform dye, and the rudiments of a darker axial line are barely distinguishable in some places; the ventral flank is a little paler, lightly washed by a yellowish rose; the antennas are blackish with the antennal tip almost black. The back is very regularly convex, and the body attenuates a lot more towards the back than towards the front; the length is 20 mm, the maximum width is 2 ½ mm. The tegument folds are disposed in the same way as in *P. nicaraguensis*, however the primary papillae are of two types: some that are sufficiently large, and others that are smaller and generally found in groups of three papillae between two big ones. These differences in regards to the type species [*P. nicaraguensis*] should be attributed to the specimen' s small size, nonetheless, the accessory papillae are numerous and well developed, whereas they are rarer in *P. nicaraguensis*. This abundance of accessory papillae is a characteristic of this variety. The clear line [midline] and the hyaline organs are a little different; the terminal cylinder [apical piece] of the primary papillae presents dimensions that are sufficiently strong. The dorsal middle side, where there are reduced papillae, is very hollow, more than in *P. nicaraguensis*. The cephalic region, and the mandibular armor reminds, from all points of view, that of this last species [*P. nicaraguensis*]. The legs are long, thin, well separated on the base, strongly reconciled. They have 29 pairs, their spinous pads are just a bit larger than those of *P. nicaraguensis*, and the 4th arch is noticeably enlarged even though it is more reduced than the precedent arch (3rd). The crural tubercles of legs IV and V are similar to the type species [*P. nicaraguensis*]; the fourth arch of the pads almost reaches its proximal border;

it is also repressed in the superior part as in *P. nicaraguensis* (Bouvier, 1902a).

Remarks: According to Bouvier (1902a), the type was donated by P. Biolley to the Museum National d'Histoire Naturelle, Paris, France, through P. Brölemann, and was included in their Catalogue of Onychophores (Bouvier, 1907b: 519). This species was briefly described by E. L. Bouvier (1902a) as *Peripatus nicaraguensis* var. *isthmicola* Bouv. and later changed to *Epiperipatus isthmicola* by Clark (1913). It must be noted that the skin pigment in the Peripatidae dissolves in alcohol (Bouvier, 1905): the color in preserved specimens is useless for taxonomy. The two main problems with this species are that the description and redescription are inconsistent, suggesting that Bouvier (1902, 1905, 1907) mixed up several species in his descriptions; and that the type locality is only approximate. The redescription (Bouvier, 1905) was based on additional specimens from "banks of Reventazón river in the Santa Clara flatlands (Atlantic versant), between 100 and 150 m of altitude". From the description we think that the site may be 10° 6' 35.70" N - 83° 31' 26.66" W, 85 m.a.s.l. They may belong to a different species: the teeth and coloration are different from the type's description. Two years later Bouvier (1907b: 519) adds specimens from other localities: (n= 1) Cachí, Cartago (col. Biolley, 1903); (n= 5) Turrialba, Cartago (col. by Anastasio Alfaro who gave them to Paul Biolley); and (n= 7) El Higuito (misspelled as El Ignito) near San Mateo, Alajuela (col. Biolley, 1906).

Oliveira, Read, and Mayer (2012b) erroneously reported the locality of *E. isthmicola* as: "Cartago, near San José", obviously misquoting Bouvier (1902a). Cartago is a different province from San José. Other reports from localities that are far from the original description site probably are misidentifications and include: Colombiana Farm, Siquirres, Limón; Finca El Uno, La Virgen de Sarapiquí, Heredia; Hamburg Farm on the Reventazón, Siquirres, Limón; Guápiles, Guápiles, Limón; Navarro, El Guarco, Cartago; Zent, Matina, Limón (Peck, 1975; Young, 1980, 1982; Monge-Nájera & Morera-Brenes, 1994). In this sense, *Principapillatus hitoyensis* was misidentified as *E. isthmicola* during a period of time by Mayer and Tait (2009), Mayer and Whitington (2009a, 2009b), Mayer, Kato, Quast, Chisholm, Landman, and Quinn (2010a), Mayer, Whitington., Sunnucks, and Pflüger (2010b), Whitington and Mayer (2011), Hering et al. (2012), Haug, Mayer, Haug, and Briggs, D. (2012) and Baer and Mayer (2012). Fortunately, there are two recent specimens that fit Bouvier's (1902a) original description and collecting area, and this allows us to establish here a neotype locality. The first specimen was collected by Elodia Sánchez Barrantes in Barrio Vasconia, City of San José (9°55'17.81" N - 84°4'18.04" W), 1 149 m altitude, 2 August 2004, in the vegetation of an urban backyard. The second specimen was collected by Adrián A. Cabrera in San José, distrito Hospital, Barrio Cristo Rey (9°55'29.90" N - 84°5'5.03" W), altitude 1 143 m, 27 May 2012, 1:46 am. It was found in a moist environment under a kitchen sink in an urban house, after heavy rains. The house was besides an abandoned backyard with vegetation. The city of San José has grown significantly (Barrientos & Monge-Nájera 2010), but in 1900 –when Biolley captured the holotype– these localities were "near San José" as he wrote (original French: *environs de San José*, see Hilje, 2013, p. 477) (Fig. 3). As expected in this group, both collection sites were near water

Fig. 3. Old (darker) and current extension of the city of San José. Circles: collection sites of *Epiperipatus isthmicola.*

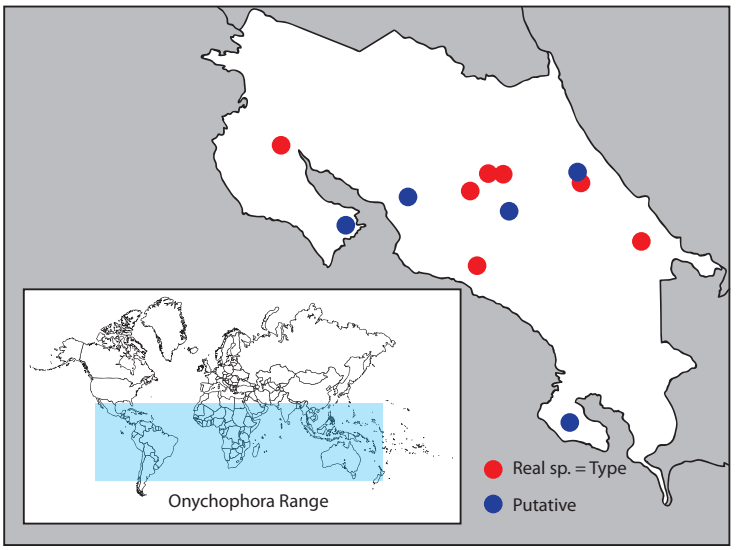

Fig. 4. Localities of all reported Onychophorans from Costa Rica, and geographic world band where the phylum currently exists.

courses (Morera-Brenes, 2012). We hereby define Barrio Cristo Rey, distrito Hospital, San José, as type locality of *E. isthmicola*, and the specimen collected there must be regarded as the neotype of these species. Since this specimen was collected by the authors, we were able to study and photograph it alive.

Epiperipatus biolleyi (Bouvier, 1902)

Synonyms: *Peripatus biolleyi*, by original designation (Bouvier, 1902b: 258); *Epiperipatus biolleyi* (Clark, 1913); (Peck, 1975: 345).

Holotype: Not designated (see Remarks).

Described type locality: COSTA RICA, "near San José, about 1 161 m of altitude" (Bouvier 1902b). The description contains imprecise and erroneous type locality data (see Remarks).

Revised type locality: Costa Rica, San José Province, Alto de la Palma, border between cantón of Moravia and cantón of Vázquez de Coronado, besides the ancient Carrillo road, Lower Montane Rain Forest in Holdridge (1978) system, approximately 10°2'52.84" N - 83°59'11.79" W, approximately 1 530 m.a.s.l., holidays (December-February) 1895 - 1896, P. Biolley col.

Language of species description: French.

Relevant taxonomic characteristics in the holotype description: "Dorsal folds are arranged normally. Primary papillae are cramped and separated one from the other by a line almost without scales; these papillae are subcilindrical and end on a narrow apical cylinder; some have a really strong basal piece and predominate strongly among the others; accessory papillae are rare, very reduced and more or less dissembled between primary papillae, on the flanks of the folds. The dorsal furrow [midline] is clear, more interrupted between the folds, lacks hyaline organs and the frontal organs are barely indicated. Two accessory teeth, where one is very small, on the outer mandibular blade, one accessory tooth on the inner blade; the mandibular saw is armed by 10 to 12 denticles. There were 28 legs on the male studied. The walking spinous pads are similar to the ones in *P. edwardsi*. Nephridial

tubercules of the legs IV and V are absolutely independent of the third arch of the spinous pads, and the forth arch is repressed and it is almost always divided in two uneven and well separated trunks. The salivary glands end in the pre-anal legs IV and V and their reservoir does not sensibly exceed the anterior legs. The prostatic vesicle is located between the preanal legs VI and VII. The crural papillae on the two pregenital pairs correspond to reduced glands, anal glands are strong, and they dilate regularly after their termination to the height of its free end, which comes up to the prostatic vesicle. Female unknown. Male size: 29 mm by 3 mm." (Bouvier, 1902b).

Remarks: According to Bouvier (1907b: 519), a type was deposited in the Museum National d'Histoire Naturelle, Paris, France. Originally described as *Periparus biolleyi* Bouv. in honor of Paul Biolley (Bouvier 1902b), the species was moved to *Epiperipatus* by Clark (1913). He did not mention color or specific location, but luckily another author did, José Fidel Tristán Fernández (Director of the Museo Nacional de Costa Rica, 1930-1932), wrote: "During the 1895 and 1896 vacations [January and February] we collected in "La Palma" [Northwest of San José] in a property that Mr. Mauro [Fernández Acuña, former Minister of Public Instruction] possessed in that place, with a relatively comfortable house.… All the species, and some new to science, that appear in various publications with the denomination "La Palma", were collected in that memorable time. There was practically no place in that region that was not registered anyway. … In one of those rotten logs [Biolley] discovered the pretty, brick colored [original Spanish: *color de ladrillo*] *Peripatus* that carries his name (Tristán Fernández, 1926, p. 38).

During field work in 2014 we learned, from local residents, that the Mauro Fernández property was in Alto de la Palma, between Moravia and Vázquez de Coronado, San José, Costa Rica, around 1 520-1 530 m.a.s.l. (aproximadamately 10° 2'52.84" N - 83°59'11.79" W). We define this locality as the neotype locality. The Onychophoran population there has been studied for some particular aspects (e.g., Mora 1991, Morera-Brenes, Herrera, Mora, & León, 1992, Monge-Nájera et al., 1993, 1994, 1996; Mora, Herrera, & León, 1996; Mayer 2006).

In this species Bouvier (1907a) included specimens from San Mateo, Alajuela (9°57'14.33" N - 84°34'6.33" W), 130-200 m.a.s.l.) and other distant localities, but they do not match the type description in teeth and color, so we think he mixed up several species. Other probably misidentified specimens include "*Epiperipatus biolleyi*" from Belize; Honduras; San Juan Pueblo; Costa Rica: "La Estrella", Parismina, fruit farm near Siquirres, Turrialba, Talamanca, San José, La Caja San José, Orotina; and Panamá: El Cermeño reported by: (Dunn, 1943; Clark & Zetek, 1946; Peck, 1975).

Peripatus ruber (Fuhrmann, 1913)

Synonyms: None.

Holotype: Not clearly designated in the original description (see Remarks).

Described type locality: COSTA RICA, "Rancho Redondo" (Fuhrmann 1913), "600 m altitude" (Fuhrmann, 1912). The description contains erroneous data and imprecise type locality data (see Remarks).

Revised type locality: COSTA RICA, San José Province, cantón of Goicoechea, distrito Rancho Redondo, Premontane Wet Forest in Holdridge system, approximately 9°57'41.17" N - 83°56'55.96" W, approximately 2 000 m.a.s.l. March 1890, P. Biolley col.

Neotype: none

Language of species description: German (and French, in a second extended version).

Relevant taxonomic characteristics in the holotype description: Of each 12 skin folds by segment, 2 are incomplete and extend

to the center of the animal. On a fold and in the middle of the primary papillae, there are generally1 to 3 papillae together, or also primary papillae. It has 30 pairs of legs. The excretory pores of the 4° and 5° pair of legs are disposed as in *P. bouvieri.* The legs always show only 4 spinous pads. The internal jaws [inner blades] have 2 accessory teeth and a denture [saw] of 11 to 13 denticles; the external jaws [outer blades] only have one accessory tooth (Fuhrmann, 1913). The species falls in the *Peripatus* Caribean group (Fuhrmann, 1912), meaning that it has three foot papillae (two anterior and one posterior).

Remark: According to Fuhrmann (1913, 1914), the type - and only known specimen– was deposited at the Musée d´Historie Naturalle de Genéve, Switzerland. It was collected in Rancho Redondo (Costa Rica), a locality that is 2 000 m.a.s.l. The label states 1 600 m, but the publication said 600 m. Fuhrmann (1913, 1914) stated that the discolored, preserved specimen was of a grayish brown but named it *ruber* ("red" in Latin) because the collector wrote that in life it was "brilliant red" [original German: lebhaft rot/original French: couleur d'un rouge vif]. We agree with Peck (1975) and Oliveira, Read & Mayer (2012b) that the "*Peripatus ruber*" from Panama and Guatemala do not belong in this species.

Macroperipatus valerioi
(Morera-Brenes & Léon, 1986)

Synonyms: None.

Holotype: Deposited in the Museo de Zoología de la Universidad de Costa Rica, San José, Costa Rica (see Remarks).

Described type locality: COSTA RICA, Río Damitas, 16 km North of Puerto Quepos, 9°34'N-84°10'W, 600 m.

Revised type locality: COSTA RICA, Puntarenas Province, cantón of Parrita, San Antonio, 4 Km from Damitas river, South side of Fila Chonta, Premontane Rain Forest in Holdridge (1978) system, basal belt transition, approximately 9°33'20.88" N - 84°11'30.83" W, approximately 300-400 m.a.s.l., 22-January- 1965, A. Wille and M. E. Bozzoli col. "under fallen log".

Neotype locality: none

Language of species description: English.

Relevant taxonomic characteristics in the holotype description: "Diagnosis: inner jaw [blade] with 2 accessory teeth, the first one more developed and with 13 denticles. Outer jaw [blade]: only one-accessory tooth. In fourth and fifth pairs of lobopods [legs], the fourth creeping pad [spinous pad] is thin and twists around the urinary tubercle, which is free and shifted to the backside. Fourth creeping pad complete or broken".

Remarks: The holotype was deposited originally at the Museo de Insectos, Universidad de Costa Rica, and latter moved to the Museo de Zoología of the same university, San José, Costa Rica. Small differences in altitude and location reflect improved GPS technology for later records.

Epiperipatus hilkae
(Morera-Brenes & Monge-Nájera, 1990)

Synonyms: None.

Holotype: Deposited in the Museo de Zoología de la Universidad de Costa Rica, San José, Costa Rica (Nr. 11-19).

Described type locality: COSTA RICA, Guanacaste, Península de Nicoya, Parque Nacional Barra Honda, Bosque de las Cascadas (10°11' N - 85°20' W), 200 m above sea level. "Col. B. Morera-Brenes 6-IV-1985 in rotten log" (see Remarks).

Revised type locality: COSTA RICA, Guanacaste Province, cantón of Nicoya, Parque

Nacional Barra Honda, Bosque de las Cascadas, Tropical Dry Forest, Moist Province Transition and Tropical Moist Forest, in the Holdridge system, 10°11'6.99" N - 85°20'22.02" W, 125 m. above sea level. "Col. B. Morera-Brenes 6 Abril 1985, in rotten log".

Neotype: none

Language of species description: English.

Relevant taxonomic characteristics in the holotype description: "Diagnosis: In fourth and fifth legs, nephridial tubercle free from third sole and only partially surrounded by the fourth arc. Each segment with 12 skin folds (seven reach ventral side) which are divided only by the dorsal midline. Primary papillae conical with rounded bases and apparently two (maximum three) "scale ranks" (=rows of scales) in the apical section. External jaw blade with two accessory teeth, the internal with one accessory tooth and 12 denticles. Diastema monolobular. Dorsal part of body dark brown with a pattern of hexagons conspicuous for their light reddish brown papillae".

Remarks: The description also included specimens from Reserva de Vida Silvestre Curú, Península de Nicoya, Guanacaste (9°46'55.90" N - 84°55'57.70" W), 20 m.a.s.l. ("C.E. Valerio, potrero Marianos, Punta Curú. Under rotten log".) We agree with Oliveira, Read & Mayer (2012b) who stated: "The species description was based on specimens from two different localities (62 km apart from each other). Thus, it might comprise a species complex, which requires revision".

Peripatus solorzanoi
(Morera-Brenes & Monge-Nájera, 2010)

Synonyms: None.

Holotype: Deposited in the Museo de Zoología de la Universidad de Costa Rica, San José, Costa Rica (UCRMZ-59-01).

Described type locality: COSTA RICA, Limón, Guayacán de Siquirres. 10°02'58" N - 83°32'31" W, 400-500 m.

Revised type locality: COSTA RICA, Limón Province, cantón of Siquirres, Guayacán de Siquirres, Tropical Wet Forest in Holdridge system, (10°03'21.38" N - 83°32'44.04" W, approximately 400-500 m.a.s.l.), 19 February 1996, A. Solórzano col.

Neotype: none

Language of species description: English.

Relevant taxonomic characteristics in the holotype description: "The following combination of characters. Dorsal primary papillae: convex and conical with rounded bases; more than 18 scale ranks. Basal piece separated from apical piece by a slight constriction. Apical section dilated, spherical and symmetric, with a basal diameter of 20 ranks; 6 or 7 scale ranks on apical pieces. Sensory bristle central, thorn-shaped, straight or slightly curved with ornamented basis. Outer blade 1 tooth, 1 accessory tooth, 1 vestigial accessory tooth (formula: 1/1/1); inner blade 1 tooth, 1 accessory tooth, 1 rudimentary accessory tooth, 9 to 10 denticles (formula: 1/1/1/9-10). Accessory tooth blunt in both blades. Four pads on fourth and fifth legs. Nephridial tubercle free from third and fourth pads, in lateral posterior position. Fourth pad is arched".

Remark: Requires revision according to Oliveira, Read & Mayer (2012b). Paratypes: Four young that were born to holotype shortly after capture, and other collected by Miguel Solano, Norberto Solano and Alejandro Solórzano, 13 August 2000. Museo de Zoología, Universidad de Costa Rica, San José (UCRMZ-60-01).

Principapillatus hitoyensis (Oliveira, Franke, Hering, Schaffer, Rowell, Weck-Heimann, Monge-Nájera, Morera-Brenes & Mayer, 2012).

Synonyms: None.

Holotype: Deposited in the Museo de Zoología de la Universidad de Costa Rica, San José, Costa Rica (MZUCR63-01).

Described type locality: COSTA RICA, Limón, Reserva Biológica Hitoy Cerere, Tropical Rain Forest, 09º40'21.56" N - 83º02'36.97" W, 300 m, 08-10 October 2005, G. Mayer col.

Revised type locality: COSTA RICA, Limón Province, cantón of Limón, Reserva Biológica Hitoy Cerere, Tropical Wet Forest, premontane belt transition, 09º40'21.56" N - 83º02'36.97" W, 300 m, 08-10 October 2005, G. Mayer col.

Neotype: none.

Language of species description: English.

Relevant taxonomic characteristics in the holotype description: "Species diagnosis: Characteristic head pattern, with three large primary papillae forming a triangle and additional conspicuous rows of primary and accessory papillae. Dorsomedian furrow flanked by one accessory papilla on each side, followed by one primary papilla; large and medium-sized primary papillae arranged out of register along dorsal midline. Males with 26-29, females with 30-32 leg pairs.

Remark: Embryonic foot projections barbed. COI and 12S rRNA sequences as in the 22 specimens sequenced. Karyotype (2n= 54, XY) with 17 pairs of acrocentric and nine pairs of metacentric/submetacentric chromosomes, and an acrocentric heteromorphic sexual pair (Oliveira et al., 2012a). This is the only Costa Rica species described with simultaneous SEM and DNA (COI y 12s ribosomal RNA genes) technology. It would be excellent if the other species could be redescribed with similar technology and standards.

DISCUSSION

Even though velvet worms occur in several areas of the world, the Costa Rican species are of particular scientific importance because they have been studied in fields other than taxonomy. There is basic work on their morphology and physiology (Monge-Nájera & Morera, 1994; Bartolomaeus & Ruhberg, 1999; Brockmann, Mummert, Ruhberg, & Storch, 1999; Mayer, 2006; Mayer & Harzsch, 2007); ecology (Picado, 1911, 1913; Young, 1980; Monge-Nájera & Alfaro, 1995); behavior (Morera-Brenes, Monge- Nájera, & Sáenz, 1988; Monge-Nájera et al., 1993, 1996); biochemistry (Mora et al., 1996; Baer, Oliveira, Steinhagen, Beck-Sickinger, & Mayer, 2014); genetics and genomics (Mora, 1991; Morera-Brenes et al., 1992; Altincicek & Vilcinskas, 2008; Podsiadlowski et al., 2008; Rota-Stabelli et al., 2010; Hering et al., 2012; Jeffery, Oliveira, Gregory, Rowell, & Mayer, 2012); phylogeography (Giribet, Edgecombe, & Wheeler, 2001; Morera-Brenes & Monge-Nájera, 2010; Murienne et al., 2014), and zooanthropology (Monge-Nájera & Morera-Brenes, 2015). The classic authority on the field, E. Bouvier, tried to improve his descriptions by adding newly collected specimens from additional areas, an error that we and other authors have made as well (e.g. Monge-Nájera & Morera, 1994; Mayer & Tait, 2009, Baer & Mayer, 2012, Hering et al., 2012). In many groups that would not be a mistake, but we now know that onychophorans have very limited geographic ranges as assumed by Monge-Nájera to produce the first cladograms of all fossil and living species (Monge-Nájera, 1995) and later corroborated by Oliveira et al., (2012a) with genetic data from Brazilian species. Bouvier (1907a) interpreted specimen differences as natural intraspecific variability in coloration, dentition and other characteristics; for example in his redescriptions of *E. isthmicola* and *E. biolleyi.*

Sumarizing all data and our field experience of 20 years in which we have seen more than 250 specimens of "*E. biolleyi"* from Cascajal and Las Nubes de Coronado

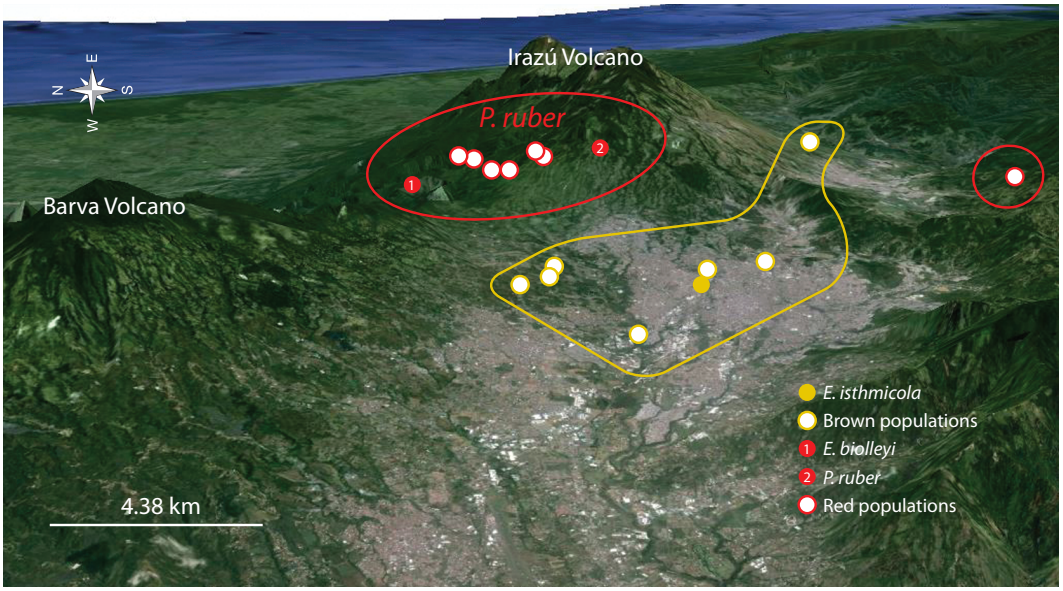

Fig. 5. Distribution of Onychophoran species found around the central volcanic complex in Costa Rica.

(which are deep brick red and do not have a diamond pattern in the back as described by Bouvier for the Surubres specimens), we think that Bouvier was wrong and that several populations of reddish onychophorans inhabit the mid elevations between Cordillera Volcánica Central and Cordillera de Talamanca (Fig. 5). They may represent more than one species and certainly are different from the brown species (some with back diamonds) found at lower elevations. Low character variation among Onychophoran species has been an obstacle for taxonomic and phylogenetic studies (Oliveira et al. 2012a). The validity of many of these taxa is uncertain and ~10 % of the described species of Onychophora, show major taxonomical problems and should be regarded as *nomina dubia* according to Mayer and Oliveira (2013). The fact that the reddish onychophorans survived the heavy ash eruptions of 1963 on the hillsides of the Irazú Volcano (see Wille & Fuentes, 1975), and that they can still be found inside homes in a modern city with a population of 400 000, is a clear evidence of the surviving power of a phylum that has been on this planet for more than 500 million years (Monge-Nájera & Hou, 1999). Here we have corrected misspelled names caused by foreign misunderstandings, a common problem with the records kept by early naturalists in Costa Rica (Hilje, 2013, p. 427). The taxonomic status of Costa Rican species needs revision and we see this article that summarizes the problems, corrects some errors and provides improved locality data, as a first step for that revision of an extraordinary group of animals.

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RESUMEN

Los gusanos aterciopelados, también llamados onicóforos o peripatos son “fósiles vivientes” de amplia distribución en los mares cámbricos pero que actualmente sólo viven en hábitats terrestres. Las únicas especies estudiadas en algún detalle son las de Costa Rica, pero su distribución

geográfica real necesitaba una revisión urgente. Para resolver este problema visitamos las localidades mencionadas en las descripciones taxonómicas originales y en las redescripciones. Estas visitas cubren un periodo de 25 años (1988-2014) e incluyen entrevistas a residentes. También examinamos todas las colecciones costarricenses (INBio, UNA y UCR); la información recopilada en mapas y libros viejos en las bibliotecas universitarias, y consultamos a expertos. Aquí revisamos críticamente la información geográfica, corregimos errores, designamos localidades de neotipo, y ubicamos poblaciones sobrevivientes después de fuertes erupciones volcánicas y procesos de urbanización de sus hábitats naturales, ofreciendo a futuros investigadores la distribución correcta geográfica de las siete especies de onicóforos descritas en Costa Rica.

Palabras clave: taxonomía, localidades, corrección de registros.

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